

CORRELATION OF CRANIAL AND DENTAL VARIABLES WITH DIETARY PREFERENCES IN MAMMALS: A COMPARISON OF MACROPODOIDS AND UNGULATES

CHRISTINE M. JANIS

Janis, C.M. 1990 3 31: Correlation of cranial and dental variables with dietary preferences in mammals: a comparison of macropodoids and ungulates. *Mem. Qd Mus.* 28(1): 349-366. Brisbane. ISSN 0079-8835.

Kangaroos and ungulate placental mammals are compared for correlations of craniodental variables with dietary type. The comparisons aim to identify those diet-related morphological variables that transcend taxonomic categories and thus represent physical constraints on craniodental design in herbivorous mammals. Kangaroos and ungulates are closely similar for most variables examined, although the absolute morphological values tend to be relatively slightly smaller in kangaroos in most cases. In addition kangaroos show a greater tendency for negative allometric scaling of these variables. Differences are mainly in molar widths, occipital height and muzzle width. To a large extent these differences, and profound differences in absolute values for variables, may related to differing modes of incision and occlusion in ungulates and kangaroos.

□ *Macropods, ungulates, craniodental design, functional anatomy, diets, phylogenetic constraints.*

Christine M. Janis, Program in Ecology and Evolutionary Biology, Division of Biology and Medicine, Brown University, Providence, Rhode Island 02912, U.S.A.; 1 July, 1988.

While it is intuitively obvious that the morphological design of animals reflects their general ecology and mode of life, few studies have attempted to quantify this apparent correlation between skeletal anatomy and behavioural ecology. Most studies of a quantitative nature have focused on carnivores (e.g. Radinsky, 1981a and b, for cranial proportions; van Valkenburgh, 1985, 1987 and 1988, for dental and postcranial proportions), or on primates (e.g. Kay & Couvert, 1984 and numerous references therein). Fewer studies are available for herbivorous mammals. Sanson (1978, 1980, 1982) has published extensively on the relation between dental wear and diet in macropodids, but has mentioned little about craniodental proportions in relation to diet. Boué (1970) noted that the lateral incisors of grazing ungulates are broader and more cup-shaped than those of browsers, and Vrba (1978) discussed the fact that grazing bovids tend to have more hypsodont cheek teeth, a shorter premolar row, a longer diastema and a deeper mandibular ramus than browsers, but neither of these studies provide quantitative evidence. However, some quantitative studies on ungulates do exist: Bell (1970) and Owen-Smith (1982) noted that grazing African bovids have relatively broader muzzles than

browsers; Radinsky (1984) discussed changes in equid cranial proportions during the evolution from a browsing to a grazing diet; Scott (1979) showed how bovid postcranial proportions may be correlated with habitat preference; and Janis (1988) demonstrated a quantitative relationship between hypsodonty index and diet in ungulates. Muzzle width and relative incisor width in all ungulates have been the subject of a more extensive quantitative analysis by Janis and Ehrhardt (1988), whose conclusions generally support those of Bell, Owen-Smith and Boué, but also show that phylogenetic history may play a role in the absolute values of these morphological variables.

The present study arose from an interest in establishing the role played by phylogenetic constraints in the design of craniodental morphology in herbivorous mammals. Preliminary studies, on the correlation between craniodental variables and dietary type in ungulates, showed that, while many variables could be correlated with diet, differences existed between ungulates of different phylogenetic lineages (e.g. between ruminant artiodactyls, suoid artiodactyls and perissodactyls — including hyracoids). Sometimes the trend was similar between animals of similar dietary types in the different lineages, but the

absolute values were different. (For example, in the correlation of basicranial angle with diet, the angles are generally more acute in artiodactyls than in perissodactyls, but nevertheless within each order grazers have more acute angles than browsers; see Fig. 9). In other cases the trend was totally different in the different lineages (for example, grazing ruminants have relatively shorter premolar rows than browsers, while grazing perissodactyls have relatively longer premolar rows; see Fig. 4).

The correlation of craniodental variables with dietary type in herbivorous mammals will be examined more fully elsewhere. In comparing macropodids with ungulates in this study my aim is to discover which morphological variables were *invariably* correlated with dietary type in herbivores, those variables might then be used to determine the diets of those fossil ungulates that lack living relatives. My rationale was as follows: kangaroos and ungulates had very different evolutionary origins, yet convergently developed into large-bodied terrestrial herbivores spanning the dietary range from omnivore to fibrous grazer. If similar trends in diet-related morphological variables could be shown to hold true for both groups, then (even if the absolute values were somewhat different) it could be assumed that the value of such a variable was somehow determined by physical constraints affecting craniodental design in all herbivores. Such variables might then be applied with confidence to fossil ungulates; by contrast those which showed different trends in living ungulates and kangaroos might be more subject to influence from phylogenetic constraints imposed on the lineages by their past evolutionary history.

MATERIALS AND METHODS

Twenty-four craniodental measurements were made on 136 species of living ungulates. These included 99 ruminant artiodactyls (families Antilocapridae, Bovidae, Cervidae, Giraffidae, Moscidae and Tragulidae), ten suid artiodactyls (families Hippopotamidae, Suidae and Tayassuidae), five camelid artiodactyls (family Camelidae) 16 perissodactyls (families Equidae, Rhinocerotidae and Tapiridae), and three hyracoids (family Procaviidae). The sample of marsupials included 52 kangaroo species (families Macropodidae and Potoroidae), one koala species (family Phascolarctidae), and three wombat species (family Vombatidae). This list does not include the complete range of living species, but



FIG. 1. Craniodental measurements. All dental lengths and widths were measured on the (occlusal) labial surface of the tooth. Other measurements were taken as follows: Lower premolar row length (PRL) and lower molar row length (MRL): along the base of the visible tooth crowns on the lateral side of the jaw. Anterior jaw length (AJL): from the boundary between molar and premolar rows to the base of the first lower incisor. Posterior jaw length (PJA): from the posterior end of the molar row to the level of the posterior border of the jaw condyle. Depth of mandibular angle (DMA): from the top of the jaw condyle to the maximum vertical depth of the angle of the mandible. Width of the mandibular angle (WMA): from the end of the molar row to the maximum linear distance on the angle of the mandible. Length of coronoid process (CPL): from the base of the jaw condyle linearly to the top of the coronoid process. Length of masseteric fossa (MFL): from the postglenoid process to the anterior-most extension of the masseteric fossa. Occipital height (OCH): from the base of the foramen magnum to the apex of the occipital ridge. Posterior skull length (PSL): from the back of the molar row to the posterior border of the occipital condyles. Orbital distance from tooth row (ODT): from the boundary between molar and premolar rows, to the closest point on the ventral border of the orbit. Length of paraoccipital process (PPL): from the top of the occipital condyles linearly to the tip of the paraoccipital process. Muzzle width (MZW): from the outer border of the junction between maxillary and premaxillary bones. Palatal width (PAW): between the protocones of the upper second molars third molars in the case of marsupials). Basicranial length (BCL): from the base of the foramen magnum to the point of angulation of the basicranial region with the face. Basicranial angle (CA): the angle between the basioccipital bone and the palate. Total jaw length = anterior jaw length (AJL) + lower molar row length (MRL) + posterior jaw length (PJA). Total skull length = anterior jaw length (AJL) + lower molar row length (MRL) + posterior skull length (PSL).

does include all living genera. Because of time constraints, and availability of specimens, some species of the very speciose genera (*Bos*, *Capra*, *Cephalophus*, *Cervus*, *Dendrohyrax*, *Gazella*, *Heterohyrax*, *Ovis* and *Procavia* in the case of the ungulates; *Petrogale* in the case of kangaroos) were excluded from the analyses. Measurements were usually made on at least six individuals of each species, and on considerably more of certain species that were better represented in collections (see Table 1). Each species was classified as a "grazer" (more than 90% of grass in the diet on a year round basis), "browser" (less than 90% of grass in the diet on a year round basis), "intermediate feeder" (10-90% of grass in the diet) or "omnivore" (taking mainly non-fibrous vegetation, including some fungal or animal material). These distinctions follow the definitions of Hofmann and Stewart (1972). Diets and body weights (expressed in kilograms) were obtained from a range of published sources for ungulates (see note following Literature Cited), and from Strahan (1983) and Lee and Cockburn (1985) for marsupials. (I am also indebted to Kathleen Scott for information on ungulate body weights, and to Peter Jarman and Tim Flannery for information on kangaroo diets and body weights).

The measurements taken on ungulates are explained in Figure 1. The way in which these measurements were modified (when necessary) in the case of the kangaroos is discussed below. All measurements, with the exception of the basicranial angle (measured in degrees by means of dividers and a protractor) were taken in centimetres with vernier or dial calipers. Measurements were obtained only from animals of specific age, as indicated by the degree of dental wear. In ungulates, measurements were made on those individuals where the last molar had fully erupted, but in which the molars did not exhibit extreme wear. Relative ages of kangaroos were treated more strictly; many of the ungulate measurements were made using the position of the first or last molar as reference points, but certain kangaroo genera exhibit molar progression, making these reference points somewhat more labile. For such macropodid taxa, care was taken to measure only those individuals that were considered to be "young adults" — i.e. those in which the last molar had fully erupted, but had not shown signs of considerable wear or of forwards progression in the jaw.

Certain variables were calculated as compounded variables. Obviously dental areas and hypsodonty index must be calculated as

compounded values, but I also calculated total skull length and total jaw length in this fashion (see legend for Fig. 1). The reason for this was that the measurements taken were originally intended for comparison of fossil mammals with living ones. Complete skulls and jaws are rare in the fossil record, although partial ones are more common. Compounded variables derived in this fashion for living mammals allow for a more direct comparison with fossil taxa, as compounded values for total skull and jaw length may be all that are available in the latter case. Hypsodonty index was calculated as the average width of the last molar (M_3 in ungulates and M_4 in kangaroos) divided by the maximum unworn height (measured on the labial border of the tooth from the base of the crown to the tip of the protoconid). In the case of the hypsodont ungulates, where the base of the unworn crown is concealed within the body of the jaw, the height of the unworn M_3 was derived from X-ray photographs (see Janis, 1988).

Ungulates and kangaroos are not directly comparable for certain variables. My designation of equivalent measurements in kangaroos (see discussion below) came both from theoretical considerations and from extensive handling of comparative material, giving confidence that any differences between the two groups in such "equivalent" variables represent differences in functional morphology. Kangaroos have four molars (or possibly five; see Archer, 1978), while ungulates have three. Rather than compare the equivalent numbered molar in each case (which would have been meaningless in terms of biology), I compared the second molars of ungulates with the third molars of kangaroos. The second molar was chosen for ungulates because this has been shown to be the best-correlated with body weight (Janis, in press). Examination of a wide range of kangaroo material led me to conclude that the third molar is the closest analogue with the second molar in ungulates, both in terms of the time of eruption in the development of the individual, and in the relative rate of wear. Both teeth are also analogous in being the "second to last from the back". Thus molar dimensions of the second molar of ungulates were compared with those of the third molar of kangaroos. The length of the lower premolar tooth-row could not be determined very easily in those kangaroo species that exhibit molar progression, (i.e. *Lagorchestes*, *Onychogalea*, *Macropus*, *Peradorcas* and *Petrogale*), since at the "young adult" stage described previously, the premolar had usually been shed. In these taxa, lower premolar row length (calculated as basal P_3

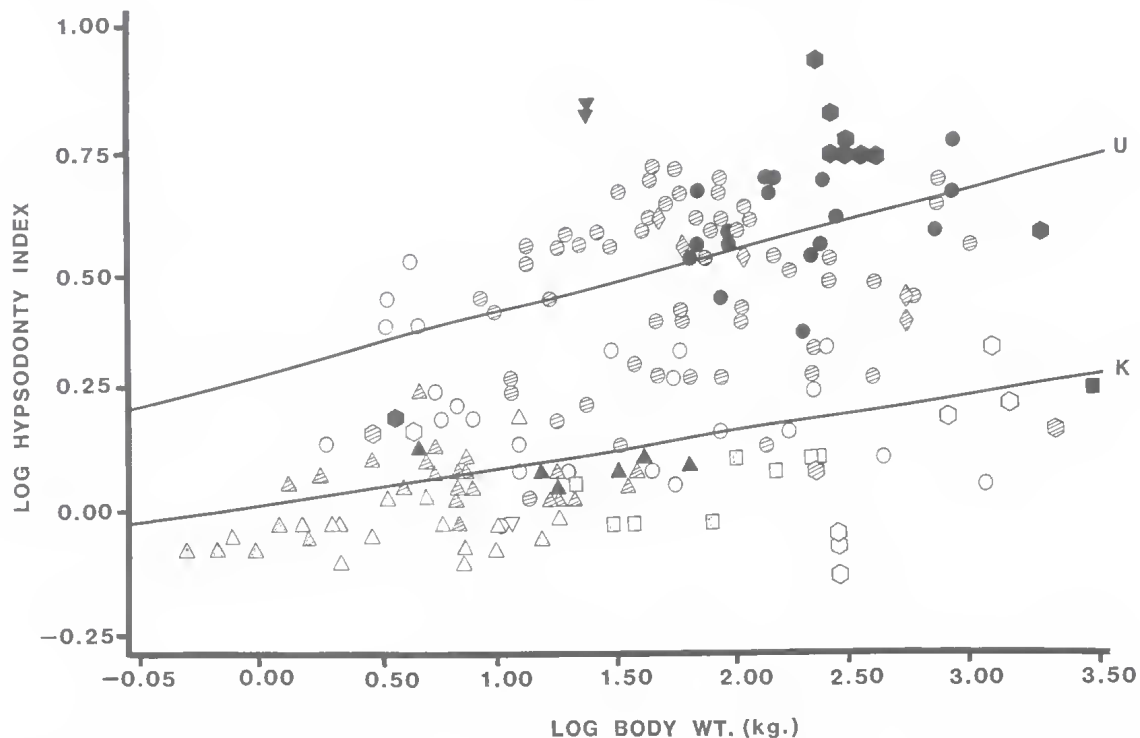


FIG. 2. Relationship of log hypsodonty index to log body weight in ungulates and kangaroos: [U — ungulates, K — kangaroos]: triangles — Macropodoid marsupials (kangaroos and potorines), inverted triangles — Phascolarctoid marsupials (koala and wombats), circle — Ruminant artiodactyl ungulates, diamonds — Camelid artiodactyl ungulates, squares — Suoid artiodactyl ungulates, hexagons — Perissodactyl or Hyracoid ungulates; open symbols — grazers, hatched symbols — intermediate feeders, closed symbols — browsers, stippled symbols — omnivores].

length) was determined from younger individuals in which the tooth exhibited little or moderate wear.

The mode of incision is very different between ungulates and kangaroos. In ungulates, the upper and lower incisors meet directly, while in kangaroos the diprotodont lower incisors fit inside the upper incisor arcade. The width of the central and lateral incisors was obtained from the lower incisors in ungulates (as ruminant artiodactyls lack upper incisors). (The relative widths of central and lateral incisors are similar for the upper and lower teeth in those ungulates, such as equids and tapirs, that retain a full compliment of upper and lower incisors). For the kangaroos, with their diprotodont lower incisors, these measurements were taken on the upper teeth. The “anterior jaw length” of ungulates was calculated as the distance from the junction of the premolar and molar row to the base of the lower first incisor. In kangaroos the premolars are usually lost in those genera that exhibit molar progression, and the lower incisor

forms part of the functional length of the lower jaw, occluding behind the upper incisors (in contrast to the direct occlusion seen in ungulates). Thus in the marsupials “anterior jaw length” was calculated as the distance between the M_1 and the tip of the lower incisor.

Plots were derived of each craniodental variable (as the dependent variable) against the body weight. In the case of sexually dimorphic species, the values and body weights of the males alone were used. All regression lines were calculated by the least squares method, and the distribution of the residuals according to feeding type around the regression line was examined in each case. Significant differences were determined by means of a *t*-test. This type of bivariate analysis, while a relatively simplistic approach, nevertheless allows for a direct comparison between ungulates and kangaroos for each morphological variable. Multivariate techniques will be used in future studies, but it is evident from these results that

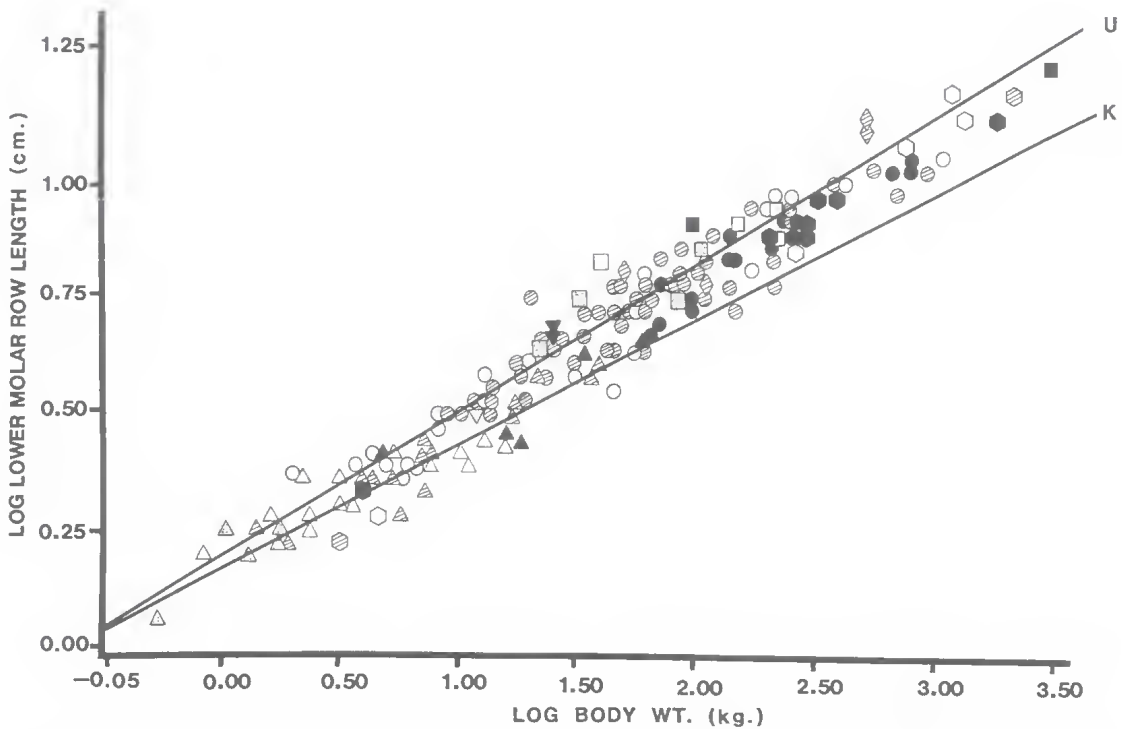


FIG. 3. Relationship of log lower molar row length to log body weight in ungulates and kangaroos (key as for Fig. 2).

many morphological variables covary with dietary type. The koala and wombat species are included on the figured plots for comparison with the kangaroos, but they were not used in the calculation of the kangaroo regression line, nor in the examination of the distribution of the residuals by dietary type around this regression line. The fact that kangaroos show a smaller number of significant differences in the distribution of the residuals is probably due to the smaller data set. The small number of true grazing kangaroos (six species in this study) is probably the reason why the residuals for kangaroos grazers rarely show a significant difference from those of the intermediate feeders.

For each variable regressed against body weight Table 2 shows: the r^2 value, the intercept, the slope, the trend in the distribution of the residuals by feeding type (including significant differences at the $P < 0.05$ and 0.01 levels), the percentage standard error (% S.E.) and a test for the allometric value of the line (i.e. whether the regression line exhibits isometry, negative allometry or positive allometry). The % S.E. reflects the extent of the scatter of the residuals around the regression line, and thus differs from the r^2 value which reflects the direct

correlation of the dependent variable with the independent variable. It is calculated by adding 2 to the log of the standard error, taking the antilog function, and subtracting 100 (see Smith, 1984). In general, a high r^2 value and a low % S.E. show that the value of the variable is closely correlated with body weight (and is thus less likely to reflect differences in dietary type), although the two functions may show considerable independent variation. The % S.E.s are generally lower for any given variable in kangaroos, which probably reflects the fact that the taxonomic diversity of the kangaroos data set is less than that for the ungulates (two families versus fourteen). In contrast, the correlation coefficients (r^2 values) are usually somewhat lower for the kangaroos, but this is probably due to the fact that the body weights of kangaroos span a smaller absolute range than those of ungulates. The regression lines were tested for allometric relations by checking if they differed significantly ($P < 0.01$) from a slope of 0.33 in the case of linear variables, or a slope of 0.66 in the case of area variables. Table 3 shows the actual mean residual values obtained for each dietary type in both ungulates and kangaroos.

RESULTS

DENTAL MEASUREMENTS

HYPSODONTY INDEX: This is a dimensionless index of relative tooth crown height, in this case obtained by dividing the unworn crown height of the last molar by the width of the same tooth. Molar crown dimensions scale isometrically with body weight in ungulates (Janis, 1988), indicating that smaller animals are neither relatively more or nor less hypsodont than larger ones. Kangaroos are much less hypsodont than ungulates of similar dietary type (see Fig. 2), even though grazing and intermediate-feeding kangaroos resemble grazing ungulates in possessing a significantly greater hypsodonty index than browsers and omnivores (significance levels for differences in residuals are detailed in Table 2).

MOLAR DIMENSIONS: As explained previously, the third molars of kangaroos were compared with the second molars of ungulates. The absolute molar dimensions are similar in both ungulates and kangaroos, but the molar lengths in kangaroos are somewhat smaller than in ungulates. This reflects the fact that the total length of the lower molar row is almost identical in both groups

(see below and Fig. 3). However, in the case of the lower molar widths, browsing ungulates have relatively wider molars than grazers, while the reverse is true (though non-significant) for kangaroos; i.e. grazers have wider molars than browsers. The same is true for the molar areas, which probably reflects the contribution of the width dimension to the calculation of the area.

Grazing and intermediate-feeding kangaroos also have a significantly longer M^3 than other feeding types, and hence have larger M^3 areas. Among ungulates, the omnivores and intermediate-feeders have a longer M^2 than other feeding types. In both ungulates and kangaroos the molar dimensions show negative allometry, in contrast to the usual mammalian isometric scaling (Fortelius, 1985). In fact, the values for the perissodactyls plus hyracooids alone do scale isometrically with body weight, but the large numbers of ruminant artiodactyls in this study have biased the results for ungulates in general (Janis, in press). Kangaroos exhibit more profound negative allometry than ungulates in the scaling of dental dimensions.

INCISOR DIMENSIONS: Absolute values for the width of the central incisors are similar in both

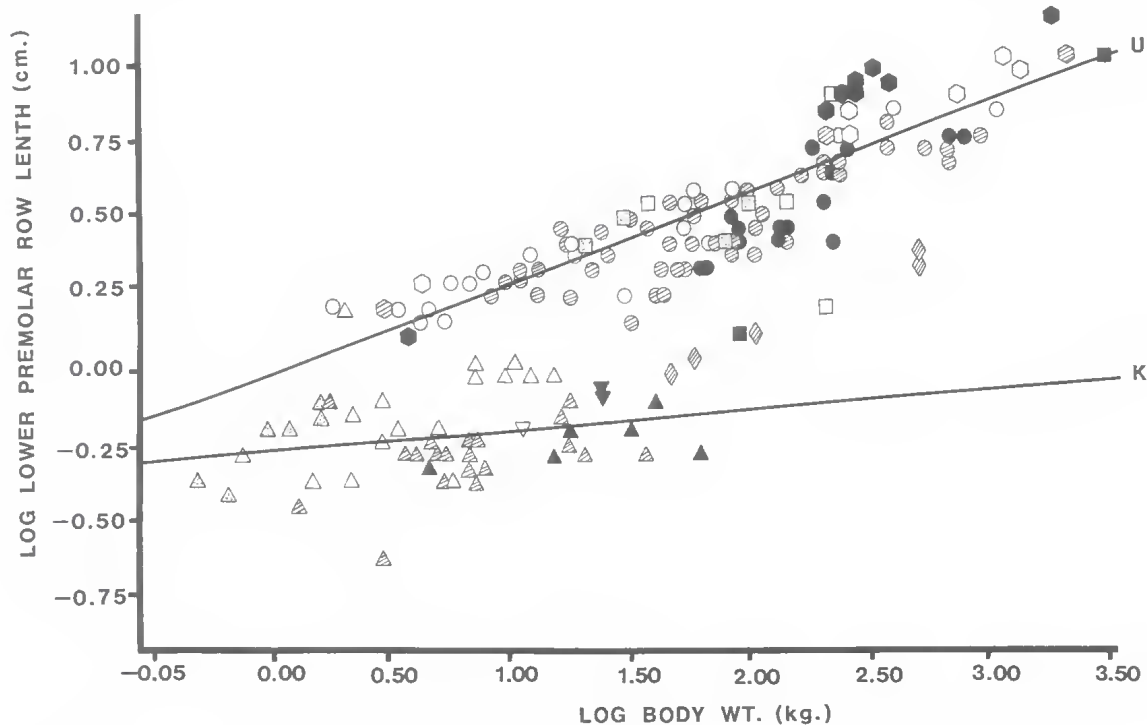


FIG. 4. Relationship of log premolar row length to log body weight in ungulates and kangaroos (key as for Fig. 2).

groups, but the width of the lateral incisor is absolutely greater in kangaroos. Browsing ungulates have relatively narrow central and lateral incisors; among kangaroos, browsers have relatively wide central incisors (although this trend is non-significant), but they resemble browsing ungulates in the significantly narrower lateral incisors. In both groups, omnivores have relatively narrow central incisors and relatively broad lateral ones (this difference being significant in both groups).

Absolute values for length of the lower molar row are similar in both ungulates and kangaroos, despite the difference in the number of molars (Fig. 3). This variable shows little variation with dietary type, and is one of the best correlates with body weight in both groups. Absolute values for length of the lower premolar row in kangaroos are much less than in ungulates, but in both groups browsers have a longer premolar row than grazers and intermediate-feeders (Fig. 4).

JAW MEASUREMENTS: Values of anterior jaw length, posterior jaw length, maximum width of the mandibular angle and total jaw length are similar for both kangaroos and ungulates, although kangaroos usually have slightly lower

values. For most of these variables, grazers have relatively larger values than browsers or intermediate-feeders. Omnivorous ungulates have relatively large values, but omnivorous kangaroos do not. The length of the coronoid process has similar absolute values for kangaroos and ungulates; in both, browsers have relatively short processes, but in ungulates intermediate-feeders have the longest processes, while in kangaroos the grazers possess the highest values. Absolute values for the depth of the mandibular angle are considerably lower in kangaroos than in ungulates. In both groups, grazers have relatively larger values than other feeding types (as would be expected to accommodate the greater volume of the masseter muscle), and omnivorous ungulates (but not kangaroos) have relatively large values (Fig. 5).

Anterior jaw length, total jaw length and the length of the coronoid process scale isometrically in ungulates, but with negative allometry in kangaroos. Maximum width of the mandibular angle scales isometrically in both. Posterior jaw length and depth of the mandibular angle scale with positive allometry in ungulates, and isometrically in kangaroos. It might be expected that the depth of the mandibular angle would show positive

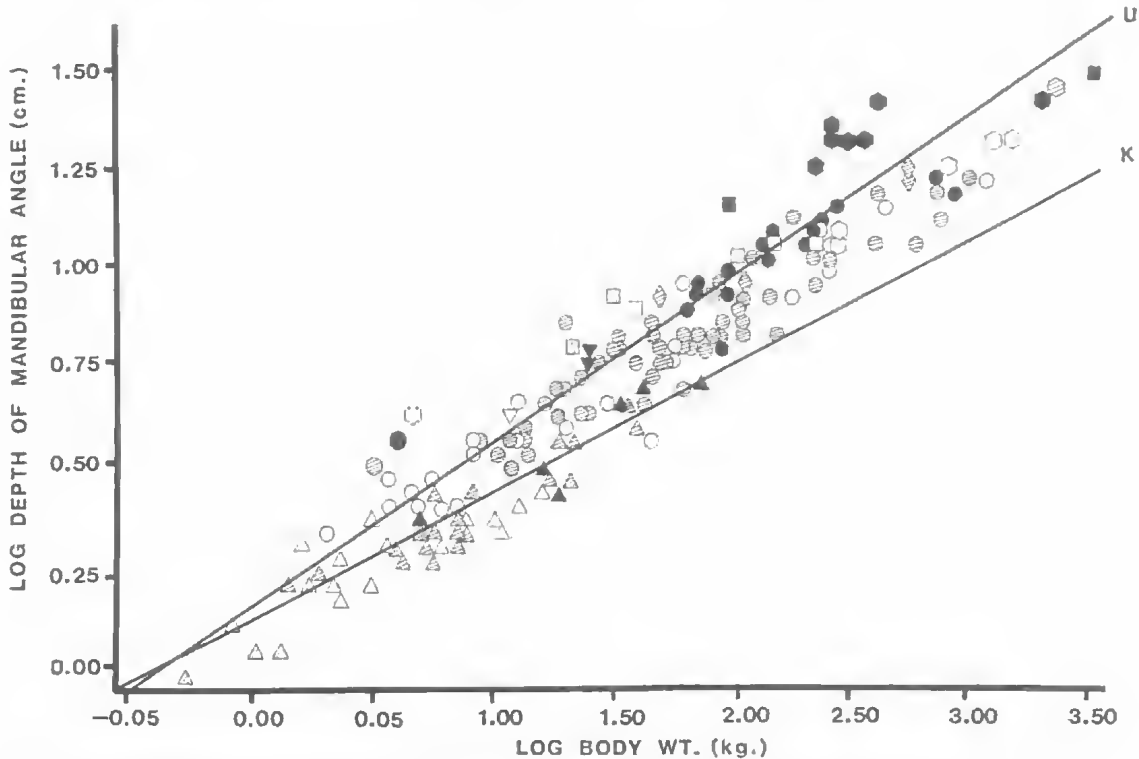


FIG. 5. Relationship of log mandibular depth to log body weight in ungulates and kangaroos (key as for Fig. 2).

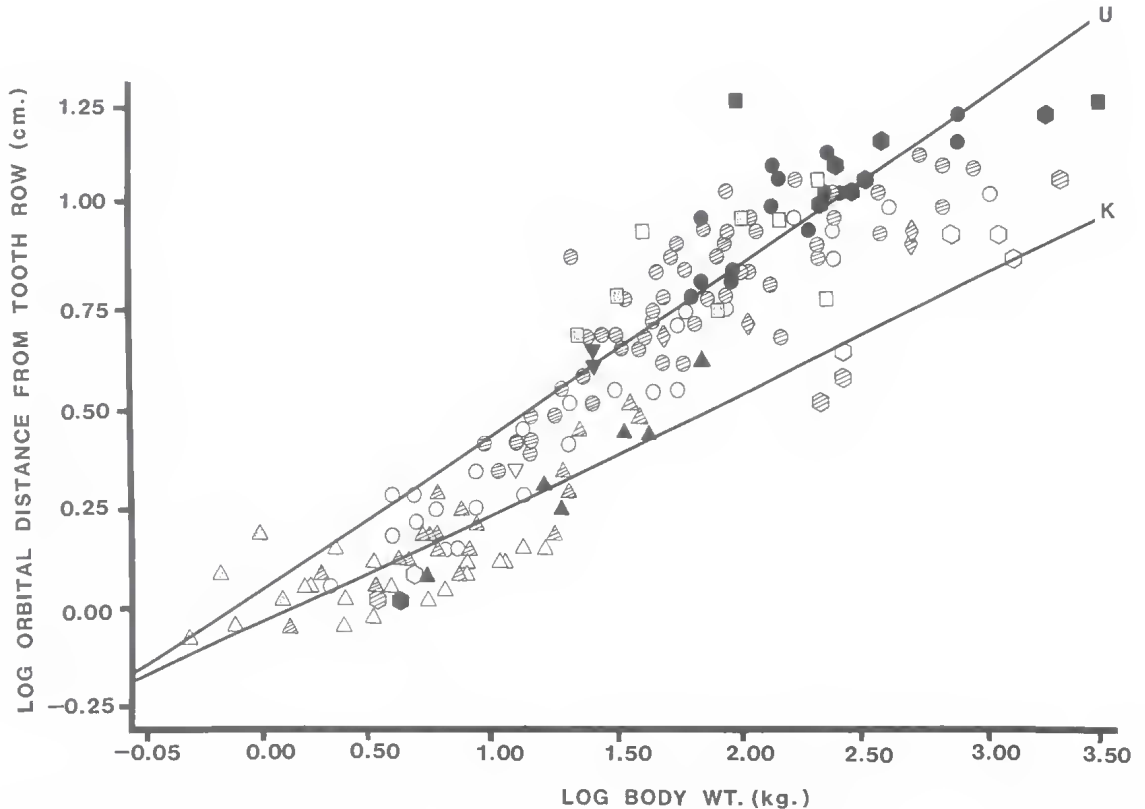


FIG. 6. Relationship of log orbital distance from tooth row to log body weight in ungulates and kangaroos (key as for Fig. 2).

allometry, since it reflects the size of the masseter muscle, which for scaling reasons would need to be relatively bigger in larger animals.

SKULL MEASUREMENTS

LENGTH MEASUREMENTS: Posterior skull length and total skull length show similar absolute values in ungulates and kangaroos (although the values for kangaroos are slightly smaller). In both groups, grazers have relatively larger values than browsers and intermediate-feeders. The absolute values of length for the paroccipital process are greater in kangaroos than for all ungulates except suids, but in both groups the paroccipital process is relatively longer in grazers than in browsers or intermediate-feeders. The occipital height of the skull in kangaroos is matched in all ungulates except suids (where it is considerably larger). However, in ungulates, browsers have larger values than other folivores (significantly larger than intermediate feeders); in kangaroos, grazers have larger values than all other feeding types (significantly larger than browsers). The distance

of the orbit from the tooth row is considerably less in kangaroos than in ungulates but, in both groups, browsers have significantly lower values than other dietary types (Fig. 6). Length of the paroccipital process scales with positive allometry in both groups. All the other skull measurements scale isometrically or with positive allometry in ungulates, but with negative allometry in kangaroos.

WIDTH MEASUREMENTS: Kangaroos show slightly lower values of palatal width than most ungulates (Fig. 7), and both groups show negative allometric scaling of this variable. Relative palatal width shows no significant correlation with dietary type in either group, (with the exception of particularly low values for omnivorous ungulates, in fact seen in all suoids). Smaller kangaroos have somewhat broader muzzles than ungulates of comparable size, but the muzzles of the larger kangaroos are relatively narrower (Fig. 8). A striking difference exists in the correlation of relative muzzle width with diet. While in ungulates the muzzles are broad in grazers, and significantly

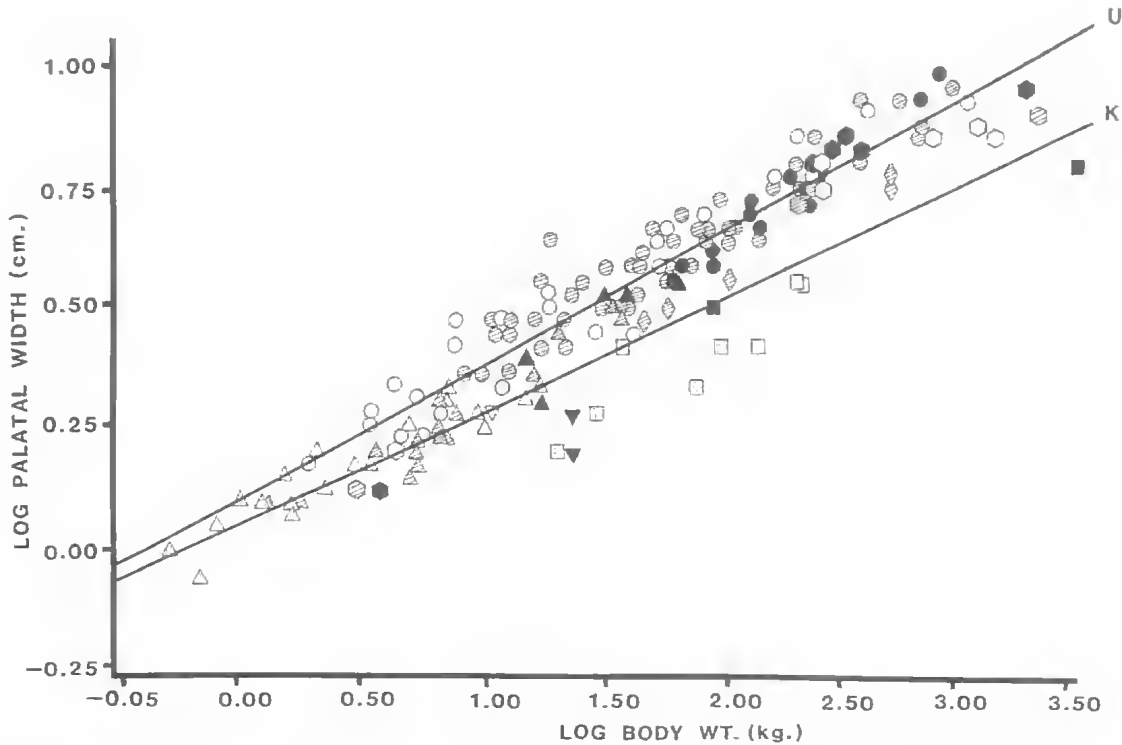


FIG. 7. Relationship of log palatal width to log body weight in ungulates and kangaroos (key as for Fig. 2).

broader than in intermediate-feeders (see also Janis and Ehrhardt, 1988), in kangaroos the muzzles are significantly broader in browsers than in other folivores. However, muzzles are relatively narrow in intermediate-feeders and broad in omnivores within both groups. Palatal width scales with negative allometry in both groups. Muzzle width scales with positive allometry in ungulates, and with negative allometry in kangaroos. However, this may merely reflect the fact that large grazing ungulates have relatively broad muzzles, while large grazing kangaroos have relatively narrow ones, and among kangaroos the broad-muzzled omnivores are the small species.

BASICRANIAL MEASUREMENTS: Kangaroos and ungulates show similar values for basicranial length; in both there is a trend (non-significant for ungulates, but significant for kangaroos) for the basicranial length to be greater in browsers. Basicranial length scales with negative allometry in both groups. Similar values are also seen in both groups for the basicranial angle (Fig. 9). However, while in ungulates intermediate-feeders have the most acute angles, in kangaroos they have the most obtuse ones. Both are similar,

however, in the fact that browsers have more obtuse angles than grazers.

DISCUSSION

Kangaroos and ungulates show a number of parallels in their adaptations of craniodental morphology to dietary type, and in many instances, they possess similar absolute values for various craniodental morphological variables. Absolute values are similar for molar widths (especially in the case of the lower molars), total length of the lower molar row, length of coronoid process, maximum width of the mandibular angle, basicranial length, and basicranial angle (although kangaroos do not show the extremes in angulation in either the acute or obtuse direction displayed in certain ungulates).

A number of convergences are seen between kangaroos and ungulates in the correlation of the relative value of craniodental variables with dietary type, irrespective of any differences in absolute values. Grazers are more likely to have the following features, in contrast with other folivorous dietary types: a larger hypsodonty

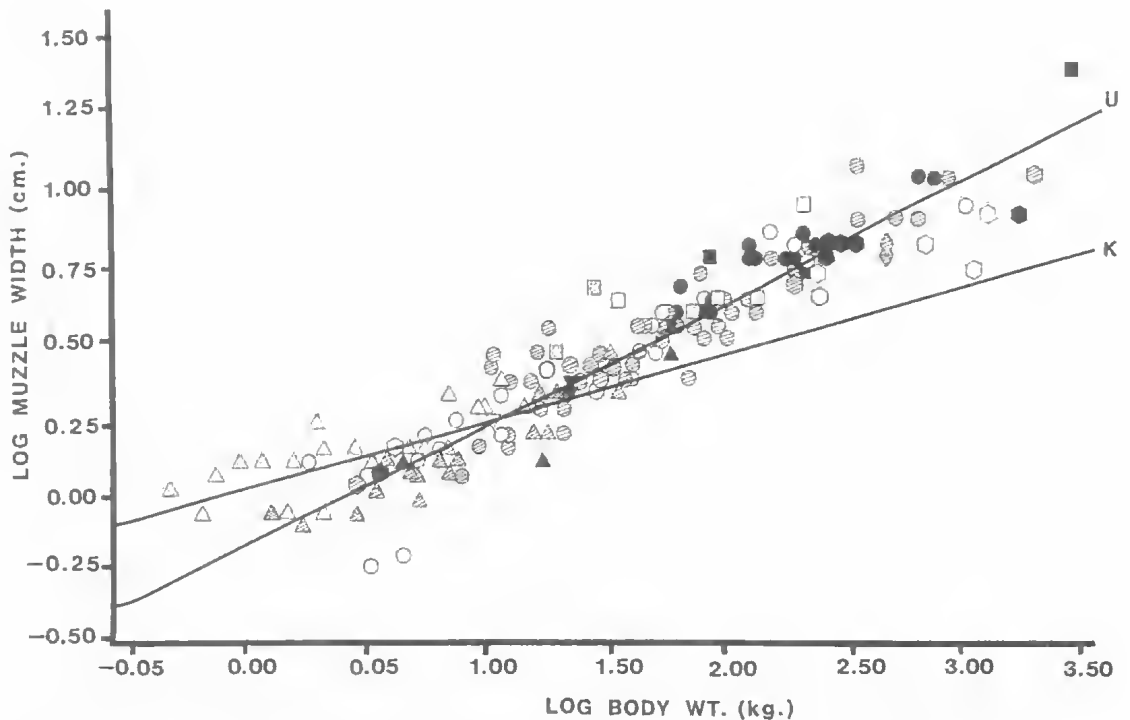


FIG. 8. Relationship of log muzzle width to log body weight in ungulates and kangaroos (key as for Fig. 2).

index; broader lateral incisors; a greater total jaw length (including a longer posterior portion to the lower jaw); a greater total skull length (including a longer posterior portion to the skull); a deeper and wider angle to the mandible; a longer masseteric fossa; an orbit that is more posteriorly displaced from the upper tooth row; a longer paroccipital process; and a fairly acute basicranial angle. In comparison with grazers, browsers are more likely to have: a low hypsodonty index; relatively narrow lateral incisors; a greater premolar row length; a shorter coronoid process; a longer basicranium; and a fairly obtuse basicranial angle. Intermediate feeders are likely to have: a moderate to high hypsodonty index; relatively narrow lateral incisors; a relatively short lower premolar row; a relatively shallow mandibular angle; a relatively short total jaw length (including short anterior and posterior parts of the jaw) and total skull length; a relatively low occiput; a relatively short basicranium; and a relatively narrow muzzle. Omnivores are likely to have: a low hypsodonty index; relatively narrow central incisors, but relatively broad lateral ones; a relatively great total skull length; and a relatively broad muzzle.

Kangaroos and ungulates show a number of absolute differences in relative craniodental proportions. The individual molars are shorter in kangaroos than in ungulates, and consequently the molar areas are smaller, which relates to the fact that kangaroos have four molariform cheek teeth, while ungulates have only three. As previously noted, the total lower molar row length is similar in both groups. The central incisors are slightly narrower in kangaroos than in ungulates, and the lateral incisors are considerably broader, which presumably relates to their diprotodont type of incision. The absolute index of hypsodonty is much less in grazing and intermediate feeding kangaroos than in ungulates of similar dietary types. This may be related to the fact that these kangaroos possess bilophodont cheek teeth, which cannot be modified to the hypsodont condition (Fortelius, 1985; Janis & Fortelius, 1988). Instead, kangaroos render their dentition more durable by means of molar progression (see Sanson, 1980). Grazing kangaroos may also be under less intense selective pressure to render their dentition more durable because of the relatively lower metabolic rate in marsupials, which means that they have to consume less food per day (see Arnold, 1985). However, it should be noted

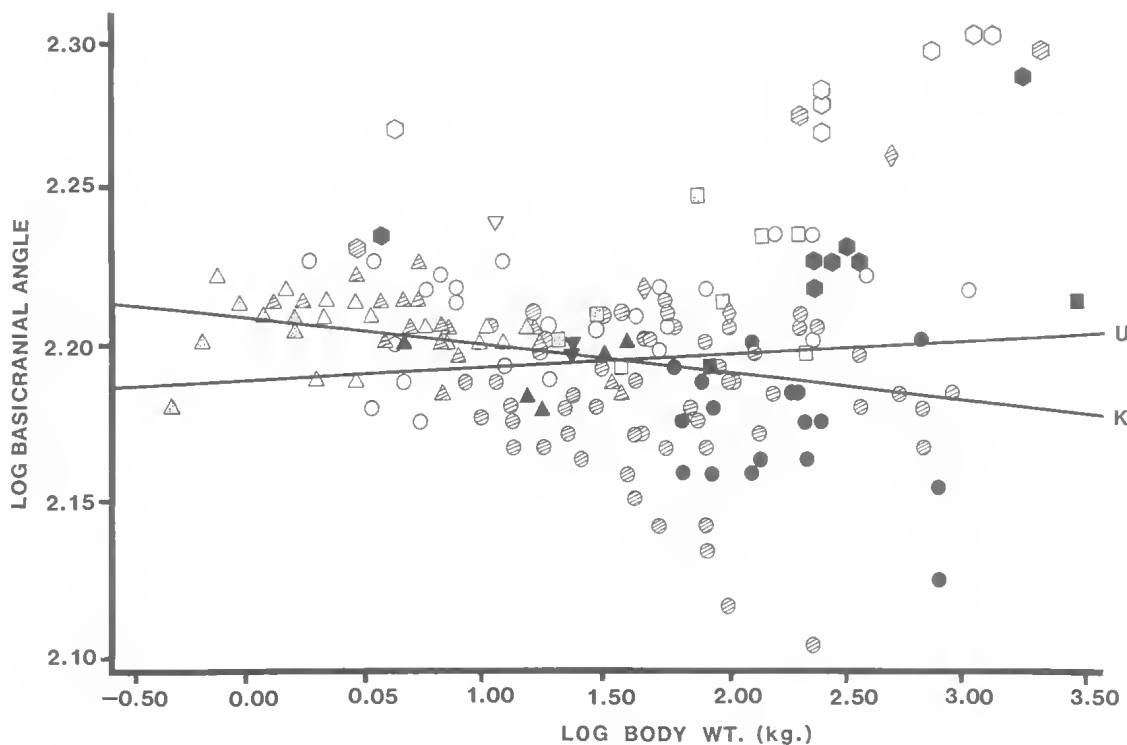


FIG. 9. Relationship of log basicranial angle to log body weight in ungulates and kangaroos (key as for Fig. 2).

that wombats are exceptional in being hypselodont (with evergrowing cheek teeth), and thus have an extremely large hypsodonty index (which should really be an index of infinity; see Fig. 2). The effective maximum height of molar crown was used in calculating hypsodonty index for wombats.

The premolar row is much shorter in kangaroos than in ungulates. This reflects the fact that adult kangaroos have a single lower premolar in contrast to the two to four seen in ungulates. Additionally, kangaroos exhibit virtually no correlation of the lower premolar length with body weight; the functional implications of this are unclear. In both groups, browsers have longer premolar rows than grazers. However, for ungulates this observation masks a difference between foregut fermenters (ruminant and camelid artiodactyls) and hindgut fermenters (perissodactyls and hyracoids). Foregut fermenters show a decrease in length of the premolar row with increasing fibre content of the diet, while hindgut fermenters show an increase (Janis, in press). Although kangaroos do have a type of forestomach fermentation (Hume, 1982), the resemblance to ruminant artiodactyls probably does not reflect a correlation with digestive physiology. A simpler, and more plausible,

explanation is that grazing kangaroos exhibit molar progression and shed the premolar at an early stage. Hence, the length of the unworn lower premolar is shorter in grazing kangaroos, as it does not form an important functional component of the cheek tooth row in the adult. (However, it should be noted that in the hindgut-fermenting phascolarctoid marsupials, the browsing koala has a relatively shorter premolar row than the grazing wombats).

In kangaroos, both total jaw length (including both anterior and posterior jaw length) and total skull length (including the posterior skull length) are slightly shorter than in ungulates. These differences may reflect differences in food handling. Most kangaroos use the forepaws to help in manipulating vegetation, and so have less need of a long skull to probe into vegetational stands. (Folivorous primates and rodents, which also manipulate food with the forepaws, also have short skulls in comparison with ungulates). Occipital height is somewhat less in kangaroos than in ungulates, and the paroccipital process is somewhat longer. Both differences probably relate to differences in the role of head-movements in association with food handling. Ungulates use

head-movements to sever vegetation gripped with the incisors (Boué, 1970), while in kangaroos the forepaws may aid in this activity. The occipital area serves as the origin for muscles that elevate the head (splenius, rectus capitus and cleidotrapezius), while the paroccipital process serves as the origin for the sternomastoid muscle, which acts to depress the head. (The large mastoid process in suids among ungulates presumably reflects their rooting behaviour with the snout).

The depth of the mandibular angle is considerably less in kangaroos than in ungulates. This could possibly reflect the lower metabolic rate of marsupials; as less food is consumed per unit time the volume of masticatory musculature does not need to be so relatively great as in ungulates. Alternatively the masseteric fossa on the jaw of kangaroos may provide an expanded area for insertion of the masseter, so that the angle of the mandible need not be as deep to accommodate the same volume of masseter muscle that would be seen in an ungulate of similar body size and dietary type. As the koala and the wombats (which do not possess this masseteric fossa) have values for this variable which are close to those of ungulates (Fig. 5), this may be the preferred explanation (see also Sanson, 1980).

The distance of the orbit from the tooth row is considerably less in kangaroos than in ungulates. This difference might correlate with the fact that kangaroos are less hypsodont than ungulates. Radinsky (1984) noted posterior movement of the orbit with increasing hypsodonty in equid evolution, and concluded that this was related to the need to house the total crown length of exceedingly hypsodont cheek teeth in horses. It is certainly true that posterior displacement of the orbit provides space for the upper molar crowns in both equids and hypsodont bovids. However, the fact that grazing kangaroos (which are not hypsodont in comparison with ungulates) show a similar relation (albeit with lower absolute values) throws doubt upon this causal explanation (as do the high values for the brachydont omnivores in both groups). In fact, some hypsodont mammals, such as rabbits and (to a lesser extent) camelids, show little posterior displacement of the orbit, and house the unerupted upper molar crowns within the anterior border of the orbit. It seems most likely that displacement of the orbit in grazing herbivores is associated with reorganization of skull proportions (such as increased acuteness of the basicranial angle and reduction in basicranial length, seen in grazers in both ungulates and kangaroos). As kangaroos show less extreme

variation than ungulates in these cranial proportions (Fig. 9), this may be the preferred explanation for the lower values for the orbital distance from the tooth row.

The palate is somewhat narrower in kangaroos than in ungulates, and the muzzle is relatively broader in small species, but relatively narrower in larger species. This narrower palate may be related to the more orthal mode of occlusion in kangaroos (Sanson, 1980). Extremely narrow palates are seen in both wombats and suines of all dietary types, and both types of mammals possess an isognathous type of dentition, implying a predominantly orthal mode of occlusion (Fortelius, 1985). As noted previously, the differences in muzzle widths with body size are probably related to the difference in size distribution of the broad-muzzled omnivorous species in the two groups.

Kangaroos differ from ungulates in the correlation of craniodental variables with dietary type in a number of ways. The molars tend to be broader in browsing ungulates, but broader in grazing kangaroos. This is probably due to the different mode of jaw occlusion. In ungulates the lower jaw moves with a broad transverse sweep across the uppers. It appears that, the more fibrous the diet, the greater the amount of transverse movement, and the relatively narrower the lower molars (Fortelius, 1985). However, the bilophodont teeth of kangaroos, and the precise fit of the lower incisors into the upper dental arcade, restricts the jaw motion to a more orthal mode. Among kangaroos the relatively wider teeth of grazers may reflect an increase in total tooth surface area for the mastication of more fibrous vegetation (also reflecting a greater total volume of food processed by the teeth per day).

The height of the occiput is greatest in omnivorous ungulates, and large in browsers; among kangaroos it is greatest in grazers and smallest in browsers. This may relate to differences among the feeding types in use of the head for obtaining food (see above). The muzzle width is greatest in grazers among ungulates, but in browsers among kangaroos. This again is probably related to differences in the modes of incision and food selection between the two groups; the implication is that grazing kangaroos are much more selective feeders than are grazing ungulates. Finally, the length of the coronoid process is greatest in intermediate-feeding ungulates, but shortest in intermediate-feeding kangaroos and greatest in grazers. This may relate to differences in use of the temporalis muscle (which inserts on the coronoid process) in kangaroos and ungulates

of different feeding types, in association with differences in the mode of occlusion. Omnivorous ungulates have high values for dental, skull and jaw lengths, while omnivorous kangaroos have low values. These differences probably reflect the fact that omnivorous kangaroos are all rather small, while omnivorous ungulates are of medium size. Thus, in addition to any scaling effects, the actual diets of the two types of omnivores are probably rather different.

Dental variables scale with negative allometry in both kangaroos and ungulates, although the negative scaling is more profound in kangaroos. Many cranial variables that scale isometrically or with positive allometry in ungulates scale with negative allometry in kangaroos. The significance of this is not clear, and it may be an artifact resulting from differences in the taxonomic diversity of the two data sets. Alternatively, differences in the ontogeny of the craniodental region between marsupials and placentals may make kangaroos more likely to exhibit negative allometric scaling of these variables (Case, pers. comm.).

CONCLUSION

Most of the craniodental differences between kangaroos and ungulates probably relate to differences in the modes of food handling and tooth occlusion. Ungulates crop vegetation with the lower incisors biting directly against the upper incisors (or a horny pad), and chew the food with transverse jaw movements, involving lophodont or selenodont cheek teeth. Kangaroos employ a precise fit of diprotodont lower incisors within an upper incisor arcade, and chew with a more orbital mode of jaw movement, involving bilophodont cheek teeth. Most kangaroos use the forepaws in handling food, while ungulates rely entirely on movements of the head to sever vegetation. Although some speculations are advanced in this paper, the role of behavioural difference in the divergent evolution of craniodental morphologies in kangaroos and ungulates remains largely unexplored.

ACKNOWLEDGEMENTS

I am indebted to the following persons and institutions for the opportunity to measure specimens in their collections: Dr M. Rutzmoser, Museum of Comparative Zoology, Harvard

University, U.S.A.; Dr R. Thorington, Smithsonian Institution, National Museum of Natural History, Washington, D.C., U.S.A.; Dr G. Musser, American Museum of Natural History, New York, U.S.A.; Drs J. Clutton-Brock and K. Bryan, British Museum of Natural History, London, U.K.; Dr A. Friday, University of Cambridge, Cambridge, U.K.; Dr L. Jacobs, National Museum of Kenya, Nairobi, Kenya; Dr E. Vrba, Transvaal Museum, Pretoria, South Africa; Dr Q. Hendy, South African Museum, Cape Town, South Africa; Dr R. Molnar and S.M. Van Dyck, Queensland Museum, Brisbane, Australia; Dr T. Flannery, Australian Museum, Sydney, Australia; Dr C. Kemper, South Australian Museum, Adelaide, Australia.

Viyada Sarabanchong collected the kangaroo data for the pilot study for this analysis, and Loren Mitchel provided invaluable assistance with data analysis. Useful information on diets and body weights was provided by Drs T. Flannery, P. Jarman and K. Scott. This paper has benefited from discussion with Drs J. Case, J. Damuth, T. Flannery, M. Fortelius, P. Jarman, K. Scott and R. Wells, and greatly benefited by comments on an earlier version from Dr William Young and an anonymous reviewer, and was supported by a National Science Foundation Grant (no. BR 84-18148) and by a Brown University Biomedical Research Grant (no. RR0708-22). Funds from the Phyllis and Eileen Gibbs Travelling Fellowship (Newnham College, University of Cambridge) permitted collection of data from the African museums.

LITERATURE CITED

- ARCHER, M. 1978. The nature of the molar-premolar boundary in marsupials and a reinterpretation of the homology of marsupial cheek teeth. *Memoirs of the Queensland Museum*, 18: 157-64.
- ARNOLD, G.W. 1985. Regulation of forage intake. p. 81-102. In Hudson, R.J. and White, R.G. (Eds), 'Bioenergetics of Wild Herbivores'. (C.R.C. Press Inc.: Boca Raton).
- BELL, R.H.V. 1970. 'The use of the herbaceous layer by grazing ungulates in the Serengeti National Park, Tanzania'. Unpublished. Ph.D. thesis, University of Manchester, England.
- BOUÉ, C., 1970. Morphologie fonctionnelle des dents labiales chez les ruminants. *Mammalia*, 34: 696-771.
- FORTELIUS, M. 1985. Ungulate cheek teeth: developmental, functional and evolutionary interrelations. *Acta Zoologica Fennica*, 180: 1-76.

- HALTENORTH, T. AND DILLER, H. 1977. 'A Field Guide to African Mammals including Madagascar'. (William Collins Sons and Co: London). [DW]
- HANSEN, R.C. AND CLARKE, R.C. 1977. Foods of elk and other ungulates at low elevation in Northwestern Colorado. *Journal of Wildlife Management*, 41: 76-80.
- HOPMANN, R.R. 1985. Digestive physiology of deer: their morphophysiological specialization and adaptation. *Bulletin of the Royal Society of New Zealand*, 22: 393-407. [D]
- AND STEWART, D.R.M. 1972. Grazer or browser; a classification based on the stomach structure and feeding habits of East African Ruminants. *Mammalia*, 36: 226-40. [D]
- HUME, I.D. 1982. 'Digestive Physiology and Nutrition of Marsupials'. (Cambridge University Press: Cambridge).
- JANIS, C.M. (1988). An estimation of tooth volume and hypsodonty indices in ungulate mammals. In Russell, D.E., Santoro, J.P. and Sigogneau-Russell, D. (Eds), 'Teeth Revisited: Proceedings of the VIIth International Congress of Dental Morphology'. *Memoires du Musum d'Histoire naturelle, de Paris, serie C*, 53: 371-91.
- (in press). Correlation of craniodental variables with body weight in ungulates and macropodoid marsupials. In Damuth, J. and MacFadden, B.J., 'Body Size Estimation in Mammalian Paleobiology'. (Cambridge University Press: Cambridge).
- AND EHRHARDT, D. (1988). Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zoological Journal of the Linnean Society*, 92: 267-84.
- AND FORTELIUS, M. (1988). On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. *Biological Review*, 63: 197-210.
- JARMAN, P.J. 1974. The social organization of ungulates in relation to their ecology. *Behaviour* 48: 213-67. [D]
- KAY, R.F. AND COUVERT, H.H. 1984. Anatomy and behaviour of extinct primates. p. 467-508. In Chivers, D.J., Wood, B.A. and Bilsborough, A. (Eds), 'Food Acquisition and Processing in Primates'. (Plenum Press: New York).
- KINGDON, J. 1979. 'East African Mammals, Vol. IIIB'. (Academic Press: London). [DW]
- 1982a. 'East African Mammals, Vol. IIIC'. (Academic Press: London). [DW]
- 1982b. 'East African Mammals, Vol. IIID'. (Academic Press: London). [DW]
- LAMPREY, H.F. 1963. Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. *East African Wildlife Journal*, 1: 63-92. [D]
- LEE, A.K. AND COCKBURN, A. 1985. 'Evolutionary Ecology of Marsupials'. (Cambridge University Press: Cambridge).
- MACKIE, R.J. 1970. Range, ecology and relation of mule deer, elk and cattle in the Missouri River Breaks, Montana. *Wildlife Monographs*, 20 [D]
- MEDWAY, G.G.-H. 1969. 'The Wild Mammals of Malaya'. (Oxford University Press: Oxford). [DW]
- OWEN-SMITH, N. 1982. Factors influencing the consumption of plant products by herbivores. p. 359-404. In Huntley, B.J. and Walker, B.H. (Eds), 'The Ecology of Tropical Savannas'. (Springer-Verlag: Berlin).
- RADINSKY, L.B. 1981a. Evolution of skull shape in carnivores. 1. Representative modern carnivores. *Biological Journal of the Linnean Society*, 15: 369-88.
- 1981b. Evolution of skull shape in carnivores. 2. Additional modern carnivores. *Biological Journal of the Linnean Society* 16: 337-55.
1984. Ontogeny and phylogeny in horse skull evolution. *Evolution* 38: 1-15.
- SANSON, G.D. 1978. Evolution and significance of mastication in the Macropodidae. *Australian Mammalogy*, 2: 23-8.
1980. The morphology and occlusion of the molariform cheek teeth in some Macropodinae (Marsupialia: Macropodidae). *Australian Journal of Zoology*, 28: 341-65.
1982. Evolution of feeding adaptations in fossil and recent macropodids. p. 490-506. In Rich, P.V. and Thompson, E.M. (Eds), 'The Fossil Vertebrate Record of Australasia'. (Monash University Offset Printing Unit: Clayton).
- SCHALLER, G.E. 1967. 'The Deer and the Tiger'. (University of Chicago Press: Chicago). [DW]
1983. 'Mountain Monarchs'. (University of Chicago Press: Chicago). [DW]
- SCOTT, K.M. 1979. 'Adaptation and allometry in bovid postcranial proportions'. Unpublished. Ph.D. thesis, Yale University, New Haven.
1983. Body weight prediction in fossil Artiodactyla. *Zoological Journal of the Linnean Society*, 77: 197-228. [W]
1985. Allometric trends and locomotor adaptations in the Bovidae. *Bulletin of the American Museum of Natural History*, 179: 197-228. [W]
- SMITH, R.J. 1984. Allometric scaling in comparative biology: problems of concept and method. *American Journal of Physiology*, 246: R152-60.
- STEWART, D.R.M. AND STEWART, J. 1970. Food preference data by faecal analysis from African plains ungulates. *Zoologica Africana*, 15: 115-29. [D]
- STRAHAN, R. 1983. 'The Australian Museum Complete Book of Australian Mammals'. (Angus and Robertson Publishers: Sydney).
- VAN VALKENBURGH, B. 1985. Locomotor diversity within past and present guilds of large, predatory mammals. *Paleobiology*, 11: 406-28.
1987. Skeletal indicators of locomotor behaviour in living and extinct carnivores. *Journal of Vertebrate Paleontology*, 7: 162-82.
1988. Trophic diversity in past and present guilds of large predatory mammals. *Paleobiology*, 14: 155-73.
- VRBA, E.S. 1978. The significance of bovid remains as indicators of environment and predation patterns. p. 247-71. In Behrensmeyer, A.K. and Hill, A.P., 'Fossils in the Making: Vertebrate Taphonomy and

Paleoecology'. (University of Chicago Press: Chicago).
 WALKER, E.P. 1983. 'Mammals of the World', 4th. ed. (The Johns Hopkins Press: Baltimore). [DW]
 WHITEHEAD, G.K. 1972. 'Deer of the World'. (Constable: London).

[DW][D] signifies reference used as source of information on ungulate diets.
 [W] signifies reference used as source of information on ungulate body weights.

TABLE 1. Complete list of species measured for craniodental dimensions.

Species	No. of Obs.	B.W. (kg.) (M/F)	Diet
UNGULATES			
ORDER ARTIODACTYLA			
Family Antilocapridae			
<i>Antilocapra americana</i>	14	55/45	I
Family Bovidae			
Alcelaphini			
<i>Aepyceros melampus</i>	23	61/45.5	I
<i>Alcelaphus buselaphus</i>	44	136	G
<i>Connochaetes gnou</i>	11	136	G
<i>Connochaetes taurinus</i>	42	239/193	G
<i>Damaliscus dorcas</i>	22	73/66	G
<i>Damaliscus hunteri</i>	10	91/86	I
<i>Damaliscus lunatus</i>	36	155/145	G
Boselaphini			
<i>Boselaphus tragocamelus</i>	6	250/170	I
<i>Tetracerus quadricornis</i>	16	17	I
Bovini			
<i>Anoa depressicornis</i>	8	156/145	I
<i>Bison bison</i>	11	865/450	G
<i>Bison bonasus</i>	4	865/450	G
<i>Bos gaurus</i>	10	1000/510	I
<i>Bos indicus</i>	6	750/450	I
<i>Bos banteng</i>	6	750/450	I
<i>Bubalis bubalis</i>	6	725/400	G
<i>Syncerus caffer</i>	23	400/320	I
Caprini			
<i>Ammotragus lervia</i>	10	113/59	I
<i>Capra ibex</i>	14	87	I
<i>Hemitragus jemlahicus</i>	10	91	I
<i>Ovis canadensis nelsoni</i>	10	73/45	I
<i>Ovis dalli</i>	8	84/59	I
<i>Pseudois nayaur</i>	10	59	I
Cephalophini			
<i>Cephalophus dorsalis</i>	7	20	B
<i>Cephalophus monticola</i>	25	5.5	B
<i>Cephalophus sylvicultor</i>	12	61	B
<i>Cephalophus spadix</i>	8	57	B
<i>Sylvicapra grimmia</i>	12	13	B
Gazellini			
<i>Ammadorcas clarkei</i>	10	31/25	B
<i>Antilope cervicapra</i>	7	45.5/29.5	I
<i>Antidorcas marsupialis</i>	29	34/28	I
<i>Gazella dorcas</i>	10	23/18	I
<i>Gazella granti</i>	10	75/50	I
<i>Gazella thomsoni</i>	29	23/18	I
<i>Litocranius walleri</i>	22	45/41	B
<i>Procapra gutturosa</i>	8	20/16	I
Hippotragini			
<i>Addax nasomaculatus</i>	4	118/104	I
<i>Hippotragus equinus</i>	18	280/260	G
<i>Hippotragus niger</i>	24	235/218	G
<i>Oryx gazella</i>	25	177/164	I
Neotragini			
<i>Dorcotragus megalotis</i>	8	9.0	I
UNGULATES			
<i>Madoqua guentheri</i>	8	3.5	B
<i>Madoqua kirki</i>	8	4.5	B
<i>Neotragus pygmaeus</i>	9	3.5	B
<i>Nesotragus moschatus</i>	20	4.5	B
<i>Ourebia ourebi</i>	14	18	I
<i>Oreotragus oreotragus</i>	18	13.5	I
<i>Raphicerus campestris</i>	31	13.5	I
<i>Raphicerus melanotis</i>	26	10	I
Reduncini			
<i>Kobus ellipsiprymnus</i>	28	227/182	G
<i>Kobus kob</i>	8	70/45.5	G
<i>Kobus leche</i>	9	100/73	G
<i>Kobus vardonii</i>	8	100/73	G
<i>Pelea capreolus</i>	14	41/23	I
<i>Redunca arundium</i>	25	68/57	G
<i>Redunca fulvorufula</i>	27	32/29.5	I
Rupicapriini			
<i>Budorcas taxicolor</i>	6	250	I
<i>Capricornis sumatrensis</i>	10	102	I
<i>Nemorhaedus goral</i>	10	27	I
<i>Oreamus americanus</i>	10	114/80	I
<i>Ovibos moschatus</i>	10	425/364	I
<i>Pantholops hodgsoni</i>	2	50	I
<i>Rupicapra rupicapra</i>	8	45/34	I
<i>Saiga tatarica</i>	8	45/40	I
Tragelaphini			
<i>Taurotragus oryx</i>	30	590/432	I
<i>Tragelaphus angasi</i>	15	114/68	I
<i>Tragelaphus buxtoni</i>	10	216/150	I
<i>Tragelaphus euryceros</i>	9	227/182	B
<i>Tragelaphus imberbis</i>	10	91/64	I
<i>Tragelaphus scriptus</i>	37	64/52	I
<i>Tragelaphus spekei</i>	12	91/57	G
<i>Tragelaphus strepsiceros</i>	28	260/170	B
Family Camelidae			
<i>Camelus bactrianus</i>	7	550	I
<i>Camelus dromedarius</i>	8	550	I
<i>Lama guanicoe</i>	10	110/75	I
<i>Lama pacos</i>	6	60	I
<i>Vicugna vicugna</i>	16	50	I
Family Cervidae			
<i>Alces alces</i>	10	450/318	B
<i>Axis porcinus</i>	8	50/35	I
<i>Blastocerus dichotomus</i>	9	140/120	I
<i>Capreolus capreolus</i>	8	35/25	I
<i>Cervus canadensis</i>	14	400/250	I
<i>Cervus elaphus scottius</i>	8	200/125	I
<i>Cervus nippon</i>	10	64/41	I
<i>Cervus unicolor equinus</i>	8	215/162	I
<i>Dama dama</i>	12	67/44	I
<i>Elaphodus cephalophus</i>	7	18	I
<i>Elaphurus devidianus</i>	17	200/150	G
<i>Hippocamelus bisulcus</i>	7	50	I
<i>Hydropotes inermis</i>	8	12/9.5	I

TABLE 1. (Continued)

Species	No. of Obs.	B.W. (kg.) (M/F)	Diet	Species	No. of Obs.	B.W. (kg.) (M/F)	Diet
UNGULATES				UNGULATES			
<i>Mazama americana</i>	10	20	B	Family Tapiriidae			
<i>Muntiacus muntjak vaginalis</i>	8	25	I	<i>Tapirus bairdii</i>	8	250	B
<i>Muntiacus reevesi</i>	8	14/12	I	<i>Tapirus indicus</i>	7	275	B
<i>Odocoileus hemionus</i>	15	91/57	B	<i>Tapirus pinchaque</i>	4	250	I
<i>Odocoileus virginianus</i>	16	58/45	B	<i>Tapirus terrestris</i>	6	240	
<i>Ozotoceros bezoarticus</i>	10	40/35	I	BORDER HYRACOIDEA			
<i>Pudu mephistophiles</i>	3	8.0/10	B	Family Procaviidae			
<i>Pudu pudu</i>	6	8.0/10	B	<i>Dendrohyrax dorsalis</i>	8	4.5	B
<i>Rangifer tarandus</i>	12	145	B	<i>Heterohyrax brucei</i>	8	3.0	I
Family Giraffidae				<i>Procavia capensis</i>	8	4.0	G
<i>Giraffa camelopardalis</i>	29	1150/1000	B	MARSUPIALS			
<i>Okapia johnstoni</i>	16	250	B	FAMILY MACROPODIDAE			
Family Hippopotamidae				Subfamily Potoroinae			
<i>Choeropsis liberiensis</i>	6	240	B	<i>Aepyprymnus rufescens</i>	9	2.1/2.5	B
<i>Hippopotamus amphibius</i>	6	3200	G	<i>Caloprymnus campestris</i>	1	0.8	B
Family Moschidae				<i>Hypsiprymnodon moschatus</i>	5	0.5	O
<i>Moschus moschiferus</i>	8	12	I	<i>Bettongia gainardi</i>	9	1.7	O
Family Suidae				<i>Bettongia lesueur</i>	6	1.7	O
<i>Babyrousa babyrussa</i>	8	85	B	<i>Bettongia penicillata</i>	7	1.3	O
<i>Hylochoerus meinertzhageni</i>	8	215	B	<i>Potorous platypus</i>	1	0.7	O
<i>Phacochoerus aethiopicus</i>	8	80/58	G	<i>Potorous tridactylus</i>	7	1.0	O
<i>Potamochoerus porcus</i>	9	78	O	Subfamily Macropodinae			
<i>Sus scrofa cristatus</i>	7	80	O	<i>Dendrolagus bennettianus</i>	2	13/10	B
Family Tayassuidae				<i>Dendrolagus dorianus</i>	9	16.5/10.5	B
<i>Catagonus wagneri</i>	6	36	B	<i>Dendrolagus goodfellowi</i>	4	7.5	B
<i>Tayassu pecari</i>	6	30	O	<i>Dendrolagus lumholtzi</i>	8	7.4/5.9	B
<i>Tayassu tajacu</i>	8	22	O	<i>Dendrolagus matschiei</i>	2	10	B
Family Tragulidae				<i>Dendrolagus ursinus</i>	2	13/10	B
<i>Hyemoschus aquaticus</i>	8	12.5	B	<i>Dorcopsis hageni</i>	4	8/5.5	B
<i>Tragulus javanicus</i>	10	2.0/3.0	B	<i>Dorcopsis veterum</i>	6	11/5	B
<i>Tragulus meminna</i>	8	7.0	B	<i>Dorcopsulus macleayi</i>	2	3.0	B
<i>Tragulus napu</i>	6	8.0	B	<i>Dorcopsulus vanheurni</i>	9	2.3/2	B
ORDER PERISSODACTYLA				<i>Lagorchestes conspicillatus</i>	11	3.0	B
Family Equidae				<i>Lagorchestes hirsutus</i>	5	2.3	B
<i>Equus asinus</i>	4	220	G	<i>Lagorchestes leporides</i>	1	1.6	B
<i>Equus burchelli</i>	57	280/235	G	<i>Lagostrophus fasciatus</i>	5	1.8	I
<i>Equus grevyi</i>	8	400	G	<i>Macropus agilis</i>	15	19/11	I
<i>Equus hemionus</i>	6	290	G	<i>Macropus antilopinus</i>	7	37/17.5	I
<i>Equus kiang</i>	6	300	G	<i>Macropus bernardus</i>	3	21/13	I
<i>Equus przewalski</i>	6	350	G	<i>Macropus dorsalis</i>	12	16/6.5	G
<i>Equus zebra</i>	19	260	G	<i>Macropus eugenii</i>	7	7.5/5.5	I
Family Rhinocerotidae				<i>Macropus fuliginosus</i>	12	35/23	G
<i>Ceratotherium simum</i>	15	3000	G	<i>Macropus giganteus</i>	8	43/27	G
<i>Dicerorhinus sumatrensis</i>	7	800	B	<i>Macropus greyi</i>	4	7.0	I
<i>Diceros bicornis</i>	23	1800	B	<i>Macropus irma</i>	7	8.0	I
<i>Rhinoceros sondaicus</i>	7	1400	B	<i>Macropus parma</i>	6	4.9/4	G
<i>Rhinoceros unicornis</i>	7	2500	I	<i>Macropus parryi</i>	15	16/11	G
				<i>Macropus robustus</i>	18	39/20	I
				<i>Macropus rufogriseus</i>	8	19.2/13.8	I
				<i>Macropus rufus</i>	16	66/26.5	G
				<i>Onychogalea fraenata</i>	6	5.5/4.5	I
				<i>Onychogalea lunata</i>	2	4.0/3.0	I
				<i>Onychogalea unguifera</i>	7	5.5/4.5	I

TABLE 1. (Continued)

Species	No. of Obs.	B.W. (kg.) (M/F)	Diet
MARSUPIALS			
<i>Peradorcas concinna</i>	7	1.4	I
<i>Petrogale brachyotis</i>	3	4.2	I
<i>Petrogale godmani</i>	5	5.0	I
<i>Petrogale inornata</i>	7	4.0	I
<i>Petrogale lateralis</i>	6	5.7	I
<i>Petrogale penicillata</i>	11	7.5	I
<i>Petrogale rothschildi</i>	2	5.25	I
<i>Petrogale xanthopus</i>	8	7.0	I
<i>Setonix brachyurus</i>	7	3.6/2.9	B
<i>Thylogale brunni</i>	6	6.0/3.6	B
<i>Thylogale billardieri</i>	6	7.0/3.9	I
<i>Thylogale stigmatica</i>	6	5.1/4.2	B
<i>Thylogale thetis</i>	11	7.0/3.8	I
<i>Wallabia bicolor</i>	8	17/13	I
FAMILY PHASCOLARCTIDAE			
<i>Phascolarctos cinereus</i>	6	11.8/7.9	B

Species	No. of Obs.	B.W. (kg.) (M/F)	Diet
MARSUPIALS			
FAMILY VOMBATIDAE			
<i>Lasiorhinus krefftii</i>	1	25	G
<i>Lasiorhinus latifrons</i>	7	25	G
<i>Vombatus ursinus</i>	6	26	G

Key to Dietary Symbols

(See text for further explanation)

“B” = browser; “G” = grazer; “I” = intermediate feeder; “O” = omnivore.

Note: Not all individuals of each species provided a complete set of all (37) measurements. (This is especially the case for those species with very large sample sizes.) Some samples include juveniles, but these are excluded from the analyses.

TABLE 2. Values for regression of craniodental morphological variables on body weight.

KEY: Int. = Intercept. % S.E. = % standard error of line. Iso = Allometric value of line (X = isometric scaling; +ve = positive allometry; -ve = negative allometry; NA = not applicable). B = Browser; G = Grazer; I = Intermediate Feeder; O = Omnivore.

A: UNGULATES								
Variable	r ²	Int.	Slope	% S.E.	Iso	Residuals of Feeding Types		
						Trend	P>0.01	P>0.05
Hypsodonty Index	0.027	0.299	0.064	69.8%	NA	G>I>B>O	G>I>B G,I>O	
M ₂ Length	0.912	-0.289	0.280	12.9%	-ve	O>B>I>G	O>G,I,B	B>I
M ₂ Width	0.853	-0.567	0.288	18.3%	-ve	O>B>I>G	O>G,I B>G	O>B
M ₂ Area	0.903	-0.855	0.567	29.7%	-ve	O>B>I>G	O>G,I,B	B>G
M ² Length	0.895	-0.276	0.280	14.3%	-ve	O>I>B>G	O>G	O>B,I I>G
M ² Width	0.892	-0.416	0.291	15.3%	-ve	O>B>G>I		O>I
M ² Area	0.913	-0.692	0.571	27.9%	-ve	O>B>I>G	O>G	O>I,B
Width of Central Incisor	0.616	-0.534	0.259	33.0%	-ve	G>I>B>O	G>B,O I>O	I>B
Width of Lateral Incisor	0.704	-1.258	0.490	56.0%	+ve	O>G>I>B	O>I,B	G,I>B
Lower Premolar Row Length	0.548	-0.003	0.268	40.6%	-ve	O>B>G>I	B>I	O>I
Lower Molar Row Length	0.911	0.221	0.280	13.0%	-ve	O>I>B>G	O>G,I,B	
Anterior Jaw Length	0.918	0.391	0.328	14.6%	X	O>B>G>I		O,G>I
Posterior Jaw Length	0.906	0.047	0.390	19.1%	+ve	O>G>I>B	G>I,B O>B	O>I
Depth of Mandibular Angle	0.852	0.200	0.377	24.7%	+ve	O>G>B>I	G,O>I,B	
Maximum Width of Mandibular Angle	0.900	0.173	0.330	16.7%	X	O>G>B>I	G>I,B	O>B>I
Length of Coronoid Process	0.637	-0.027	0.306	38.4%	X	I>G>B>O	O>I I>B	G>B,O I>O
Total Jaw Length	0.946	0.716	0.332	11.7%	X	O>G>B=I	O>I,B	G>I
Length of Masseteric Fossa	0.927	0.465	0.330	13.8%	X	G>I>B>O	G>B	G>I>O I>B,O
Occipital Height	0.854	0.234	0.315	19.9%	X	O>B>G>I	O>B>I O>G	G>I

TABLE 2. (Continued)

A: UNGULATES								
Variable	r ²	Int.	Slope	% S.E.	Iso	Residuals of Feeding Types		
						Trend	P > 0.01	P > 0.05
Posterior Skull Length	0.937	0.373	0.354	13.8%	+ ve	G > O > I > B	G > I, B	
Orbital Distance from Tooth Row	0.751	0.047	0.388	36.8%	+ ve	O > G > I > B	G, I, O > B O > I	O > G > I
Length of Paroccipital Process	0.845	-0.168	0.373	25.0%	+ ve	O > G > I > B		
Total Skull Length	0.954	0.811	0.328	10.7%	X	O > G > B > I	O, G > I	O > B
Muzzle Width	0.863	-0.191	0.388	24.2%	+ ve	O > G > B > I	O, G > I	O > B
Palatal Width	0.854	0.084	0.290	18.3%	- ve	I > B > G > O	G, I, B > O	
Basicranial Length	0.881	0.407	0.283	15.6%	- ve	B > G = I > O		
Basicranial Angle	0.004	2.191	0.004	9.4%	NA	B > O > G > I	B > G, I	O > I
B: KANGAROOS								
Hypsodonty Index	0.095	0.005	0.054	19.7%	NA	I > G > O > B	G, I > B I > O	G > O
M ₂ Length	0.871	-0.369	0.269	11.9%	- ve	G > I > O > B		
M ₂ Width	0.815	-0.506	0.220	12.2%	- ve	O > G > I > B		
M ₂ Arca	0.868	-0.875	0.489	23.3%	- ve	G > O > I > B		
M ³ Length	0.855	-0.351	0.268	12.7%	- ve	G > I > B > O	I > O	I > B G > O
M ³ Width	0.834	-0.476	0.256	13.2%	- ve	B > O > I > G		
M ³ Area	0.888	-0.827	0.524	22.5%	- ve	G > I > B > O		I > O
Width of Central Incisor	0.201	-0.561	0.186	50.0%	- ve	B > G > I > O		G, B, I > O
Width of Lateral Incisor	0.670	-0.647	0.341	29.7%	X	G > O > I > B >	O, I > B	G > B
Lower Premolar Row Length	0.023	-0.239	0.049	41.9%	NA	B > O > G > I	B > I	B > G
Lower Molar Row Length	0.905	0.187	0.246	9.1%	- ve	G > I > B > O		
Anterior Jaw Length	0.860	0.307	0.289	13.5%	- ve	G > O > I > B		G > I, B
Posterior Jaw Length	0.927	0.199	0.311	9.9%	X	G > O > I > B		
Depth of Mandibular Angle	0.868	0.123	0.309	14.0%	X	G > I > B > O		
Maximum Width of Mandibular Angle	0.941	0.215	0.311	8.9%	X	G > I > B > O		
Length of Coronoid Process	0.862	0.004	0.277	12.7%	- ve	G > O > B > I		
Total Jaw Length	0.933	0.713	0.283	8.6%	- ve	G > I > I > B	G > I	
Length of Masseteric Fossa	0.944	0.464	0.249	6.9%	- ve	G > O > I > B		
Occipital Height	0.912	0.248	0.236	8.4%	- ve	G > O > I > B	G > B	
Posterior Skull Length	0.938	0.400	0.271	7.9%	- ve	O > G = B > I	O, B > I	
Orbital Distance from Teeth Row	0.706	-0.035	0.269	20.8%	- ve	O > G > I > B	O, I > B	G > B O > I
Length of Paroccipital Process	0.934	-0.104	0.433	13.2%	+ ve	G > I > B > O	I > O	B > O
Total Skull Length	0.935	0.784	0.271	8.1%	- ve	G > O > B > I		
Muzzle Width	0.566	-0.026	0.214	22.5%	- ve	O > B > G > I	O, B > I	O, B > G
Palatal Width	0.919	0.056	0.266	8.9%	- ve	G > B > O > I		
Basicranial Length	0.926	0.396	0.271	8.6%	- ve	B > I > G > O	B > I, O	B > G
Basicranial Angle	0.199	2.218	-0.011	2.3%	NA	I > B > G > O		I, B > O